Understanding plant invasions

Ordoñez Gloria, Alejandro

8 Synthesis: are we closer to understanding and predicting invasions?

Alejandro Ordoñez Gloria[ab]

[a] Community and Conservation Ecology Group, University of Groningen
[b] Correspondence author. E–mail: A.Ordonez.Gloria@rug.nl

8.1 Introduction

Introduction of non–native species is one of the main drivers of global change (Vitousek, Mooney et al. 1997) causing major changes in ecosystem processes and functioning (Le Maitre, van Wilgen, Gelderblom, Bailey, Chapman & Nel 2002, Mooney & Hobbs 2000, Vitousek et al. 1997, Vivrette & Muller 1977, Westbrooks 1991) in addition to significant economic and biodiversity losses (Pimentel, Zuniga & Morrison 2005, Sax & Gaines 2003). The importance of the problem highlights the needed for methods that accurately discriminate which plants, once introduced, will be successful and could possibly become invasive.

Invasion biologists have tried to address this problem by asking one of two important questions: i) which species are invasive (a species–based approach), and ii) which habitats are most likely to be invaded (a community–based approach). To address the first question, most works have aimed to determine a broad list of traits that can be used to describe which species will be successful in a new environment. This idea of describing the characteristics of the ”average successful alien” builds from Baker, Stebbins & International Union of Biological Sciences’s (1965) description of the ”ideal weed” (e.g. plants with ruderal strategies). Although, due to the idiosyncrasy of the invasion process, some authors believed that such a list was not possible (e.g. Alpert & Simms 2002, Roy 1990); later works, inspired by Rejmanek’s (1996) *”Theory of seed plant invasiveness”* have shown (by the use of multi–species comparisons) that successful aliens do appear to have some traits in common (e.g. Cadotte & Lovett-Doust 2001, Goodwin, McAllister & Fahrig 1999, Hamilton et al. 2005, Lake & Leishman 2004, Ordonez et al. 2010, Pyšek & Richardson 2007, van Kleunen et al. 2010).

Efforts to answer the second question have yielded descriptions of the characteristics that make a given area intrinsically vulnerable to invasions. Some of the proposed characteristics are low site diversity (Elton 2000, Levine et al. 2004, Maron & Vila 2001); availability of empty niches (Elton 2000, Hierro et al. 2005); release from natural enemies (Colautti et al. 2004, Darwin 1866, Torchin & Mitchell 2004); introduction of novel weapons to the target area (Callaway & Aschehoug 2000, Callaway & Ridenour 2004); high resource availability (Blumenthal 2005, Davis et al. 2000) and high disturbance frequency (Lozon & MacIsaac 1997).

It’s clear that each of these approaches provide complementary answers to the *”what drives invasions”* question. Therefore, any progress towards a general theory of plant invasiveness can only been achieved by pooling evidence from both the species invasiveness and community invasibility approach. Some efforts to make this link (e.g. theory of seed plant invasiveness Rejmanek (1996); fluctuating resources theory of invasibility **?**; niche opportunity: Shea & Chesson (2002); or state factor models Barney & Whitlow (2008) among others) have aimed to explicitly linking the relation between the characteristics/traits of a given aliens and the ecological–resource–enemy–evolutionary–environmental setup an alien species will face on a particular location. This dissertation is based on this perspective; aiming to address by the use of a global scale multi–species, target area, native–alien comparison approach, how auto-ecological, evolutionary and environmental factors affects invasions success.

8.2 Attributes of success: What traits tell us about invasions?

To date, most works aiming to determine a link between traits and invasion have focused their efforts on profiling the "average successful alien" (***Table 8.1***). Although, some generalisations have been found (e.g. aliens have faster grow rates, higher leaf nutrients contents and specific leaf areas, shorter life cycles, devote more resources to reproduction and produce more seeds that are better dispersed and germinate faster) it is clear that any benefit yield from expressing a given attribute (or set of them) would be contingent on the biological–evolutionary–abiotic setup a species faces.

Ecological and physiological literature has shown how fitness and performance of a given species is determined by both its' traits, and the functional and evolutionary relation to the community it is embedded in (Lavorel & Garnier 2002, Marks & Lechowicz 2006, Marks 2007, Tilman 1982). This link between traits–performance–fitness provides a methodological framework to compare alien and native species worldwide. This is clearly the case for the group of traits used in this dissertation (i.e. Specific leaf area, photosynthetic capacity, leaf nitrogen content, individual seed weight, and typical maximum height), given their influence on resource acquisition, growth, herbivory risk, r–K strategy, reproductive output, light competition, risk of breakage and respiration costs (Falster & Westoby 2003, Moles & Westoby 2006, Moles et al. 2009, Westoby et al. 2002, Wright et al. 2004). Furthermore, each of these traits is linked to a particular ecological strategy (i.e. Leaf economics, seed mass-seed output trade-off, and canopy height, as proposed in Westoby et al. 2002, Westoby & Wright 2006) representing how a species secure carbon profit during vegetative growth, ensure gene transmission into the future and interacts with both the environment and other co–occurring species.

This work has shown how alien species, as a group, differ in individual traits (***Chapter 3*** and ***4***) each one representing an approximately independent axis of trait/strategy variation. These differences also hold for comparisons based on the multivariate trait composition (SLA–H_{max} –SWT 3D or 2D spaces, ***Chapter 3***) and their positioning along the "leaf economics spectrum" (***Chapter 5***). Aliens location in both uni– and multivariate trait–space, indicated how non–natives had the tendency to occupy regions clustered towards the edge of at least one of the evaluated dimension, when compared to natives (***Chapter 3*** and ***5***). Therefore, alien species could be considered as a biased sub-sample of species with regard to the evaluated traits, such that they tend to express greater leaf traits (SLA, N_{mass}, A_{mass}, as shown in ***Chapter 3*** and ***5***), lower maximum height or/and smaller seed size (as shown in ***Chapter 3*** and ***4***). These results indicate that the observed trend of global differentiation relate to one (or both) of two possible mechanisms determining the success of alien species: i) the idea of limiting similarity, so that alien species are less likely to establish in communities that are dominated by species with similar traits (Abrams 1983, Hutchinson 1959); and ii) phenotypic attraction hypothesis, so that alien species are more likely to establish in communities with congenerics (Daehler (2001) and Diez et al. (2009); and tested in ***Chapter 6***)

When aliens where compared to natives co–occurring in the same area, both a significant alien–native trait differentiation on individual traits and multi–trait composition was detected (as illustrated by the significant random intercepts of linear mixed

Table 8.1 Synthesis of results from comparative and congeneric studies on traits promoting invasiveness in plant. Traits not addressed in a particular study (Multi–species comparative or congeneric/confamilial paring) are indicated by empty cells. Table based on references compiled in Pysek & Richardson (2007).

Group of traits	Trait	Multi–species comparative studies	Congeneric–Confamilial studies
Morphological	Biomass		Ambiguous
	Plant height	Promotes invasiveness	Promotes invasiveness
	Vegetative spatial growth	Promotes invasiveness	Promotes invasiveness
	Leaf number		Ambiguous
	Leaf morphology, canopy structure	Ambiguous	
Physiological	Photosynthetic rate/capacity		Promotes invasiveness
	Water, N and P use efficiency		Promotes invasiveness
	Specific leaf area	Promotes invasiveness	Promotes invasiveness
	Leaf area ratio		Promotes invasiveness
	Total leaf area		Ambiguous
	Seedling relative growth rate	Ambiguous	Promotes invasiveness
	Growth rate, allocation to growth		Promotes invasiveness
Reproductive	Self-compatibility	No pattern	Limited info
	Breeding system	Some types are related	
	Pollen vector	No pattern	
	Time of flowering	Early/longer flowering	Early/longer flowering
	Fecundity		Promotes invasiveness
	Propagule size	Promotes invasiveness	Limited info
	Dispersal mode and efficiency	Ambiguous	Promotes invasiveness
	Germination ability		Promotes invasiveness
	Seedling survival and establishment		Promotes invasiveness
	Seed dormancy/bank/longevity/size	Limited info	Promotes invasiveness

models ***Chapter 2***, ***4*** and ***5***). Together, these results indicate a context dependence on alien–native performance differences, and how opposite and balancing mechanism might act at different spatial scales. Specifically, evaluating the effect of scale on these differences showed a consistently unbalanced distribution across a scale gradient ranging from species to regions. These comparisons suggest that the process causing trait differentiation (i.e. limiting similarity) mainly acts at the smallest scale of analysis (74 to 94% of the trait differentiation variability is captured at the species level, as shown in ***Chapter 4***). Comparisons at larger scales capture only a marginal fraction of the variability in trait differences (0 to 17%); indicating how at these scales ecological factors drive analysed traits towards convergence (i.e. phenotypic attraction). From this is clear that according to scale of analysis, evaluated attributes could show either patterns of divergence (e.g. plot–community scales) or convergence (e.g. areas–biomes–regions).

When focusing only at a community scale, the more dissimilar (functionally and/or phylogenetically) an alien species is to the native species community pool, the greater its chances are that it will be successful when introduced (as shown in ***Chapter 3***, ***4*** and ***5***; and reviewed by Diez et al. 2009, Pyšek & Richardson 2007, van Kleunen et al. 2010). We emphasise that, although the summarised patterns of differentiation (in uni– or multivariate trait spaces) seem rather small in absolute (15 to 26% ***Chapter 3***) or relative terms (2 to 16% ***Chapter 4*** and ***5***); it is very difficult to predict how big a trait difference should be in order to be of ecological relevance (e.g. in competition), as hardly any data on this are available in the literature. In fact, the classic principle of competitive exclusion (Gause 1934) can be interpreted such that very small but consistent trait differentiation among species, competing for a single resource, will always lead to full competitive displacement.

The idea of functional dissimilarity between aliens and natives has been tested previously by focusing on how a particular attribute of an alien species differs from those of co–occurring natives (as discussed in the introduction and summarised in ***Table 8.1***). When comparing the findings from these works amongst them, and with those of this dissertation, is clear that any discrepancy will emerge from the differences in the spatial and/or phylogenetic scale of the comparisons. This indicate how formulating the alien–native comparison in an explicit scale context (spatial and taxonomic/phylogenetic) is essential for revealing and understanding both the mechanisms behind the observed alien–native trait similarity/dissimilarity patterns, and the relation between these differences and the success of an introduced species.

Lastly, the comparison criteria might also play an important role on the observed trait convergence–divergence patterns (as discussed in the introduction and ***Chapter 6***). For example, in the case of comparison with a native community pool (multi–species contrasts as presented in ***Table 8.1***) aliens are expected to show trait differentiation, due to niche filing, competitive exclusion and limiting similarity. On the contrary, comparisons within a similar growth form, functional group or between closely related species (experimental paring of species based on functional, phylogenetic or taxonomic similarity, as presented in ***Table 8.1***) traits of aliens would tend towards convergence with the compared species of group.

It seems counter-intuitive that successful aliens are dissimilar to most natives, but

similar to closely related natives (in a functional or phylogenetic space). This apparent paradox can be explained (as discussed in ***Chapter 6*** and by Scheffer & van Nes 2006), by a balance between niche filing–adequacy mechanism. In un–invaded conditions, species are spread out in a trait/niche space (as assumed by limiting similarity and niche partitioning theory), making the intermediate positions between native species open niches; and obviously the best places for new invaders. However, if the introduced non–native is very similar in a functional space (or in a community were resident species traits/niches are closely packed), the areas between species traits/niches are unsuitable locations (MacArthur & Levins 1967*b*, Scheffer & van Nes 2006), making the invasion of areas close to the native–pair a more viable option. The balance between these two forces would then lead to the observed pattern of alien species occurrence in a given community. Specifically, areas between natives in a given area can only be invaded by highly competitive species (the so called super invaders; as discussed in Daehler 2003, Richardson & Pyšek 2006). Whereas the areas between functionally close species are relative windows of opportunity where even relatively weak aliens can be successful if they are functionally similar to those natives. A point to emphasise here is that this balance can be easily broken by the random introduction of certain species (with unusual high competitive ability) and intrinsic native–native and alien–native differences in overall competitive power.

8.3 Mechanisms responsible for aliens' trait differentiation

As an alien species is introduced to a new region/habitat, it must overcome a set of environmental and biological barriers (e.g. seed germination, seedling establishment, physiological tolerances, demographic stochasticity, and biotic interactions) all of which restrict its' demographic and physiological success (Pyšek & Richardson 2007, Richardson & Pyšek 2006). In addition, it is almost inevitable that introduced plant populations will loose most of its natural enemies (specialist), mutualism and competitors; while at the same time establish new interactions with those species occurring in the new area (Levine et al. 2004, Mitchell et al. 2006, Mitchell & Power 2003, Rejmanek et al. 2005). From this perspective, trait differentiation from the existing native species poll would allow aliens to succeed in their introduced range by reducing possible competitive interactions with the native community. Meanwhile, similarity to natives would allow aliens to overcome the restrictions imposed by environmental factors (***Fig. 8.1***). Resulting form this balance, trait segregation between co–occurring native and aliens (as pointed out in ***Chapter 3***, ***4***, and ***5***) would trigger dissimilarities in performance, competitive ability, and growth–reproduction dimensions, between introduced and all native plants on a site. Meanwhile, trait similarity at larger scales (as pointed out in ***Chapter 4***) would be the result of habitat filtering and niche conservatism (***Chapter 7***).

The emerging question is then, *how aliens manage to obtain these differences in traits?*. Several possible explanations/mechanism have been proposed to answer this question. These range from phenotypic plasticity, mutation–hybridisation–polyploidy or the fact that aliens have the same extreme values in their home range (this last one

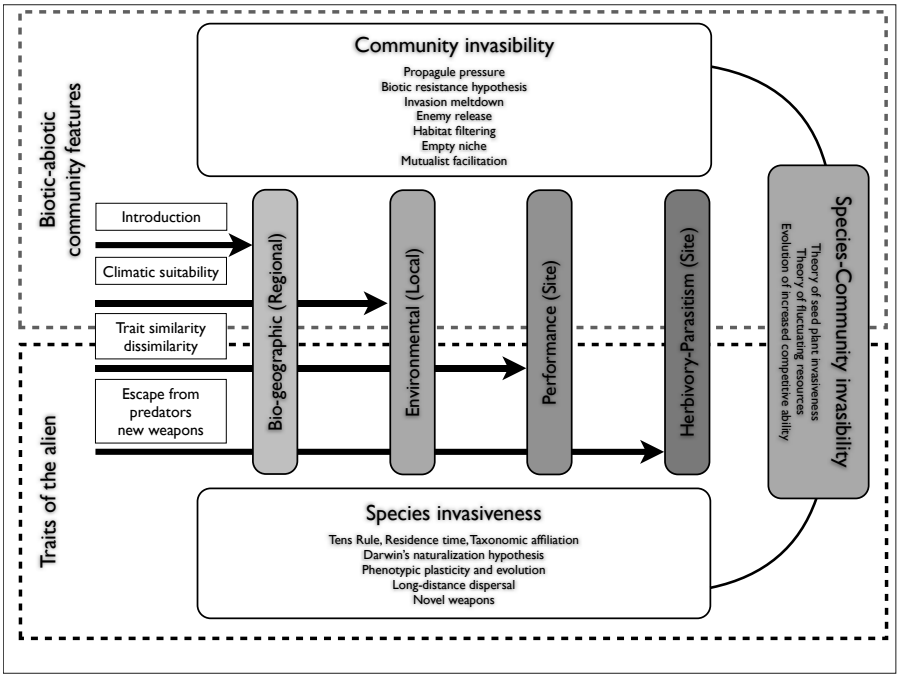

Figure 8.1 The "alien introduction continuum" conceptualises the various barriers that a plant must overcome to establish a viable in a new environment (figure is adapted from Richardson & Pysek (2006)). Understanding of the dynamics of plant invasions requires insights on traits of the plant (elements of species invasiveness) and features of the environment (components of community invasibility), but neither aspect can be fully evaluated without reference to the other. A predictive framework for invasion biology should be a holistic combination of these factors in addition to consider the spatial and phylogenetic scale of the contrast.

evaluated in ***Chapter 2***). Supported on evidence coming both from the results presented in this dissertation, and those of related fields [e.g. theories of trait/functional diversity evolution Ackerly (2003), resource competition theory Tilman (1982) and growth rate hypotheses Elser, Acharya, Kyle, Cotner, Makino, Markow, Watts, Hobbie, Fagan, Schade, Hood & Sterner (2003)] some of the possible mechanisms generating the observed trends in alien species traits are now discussed. First, lets' focus on the role of phenotypic plasticity, niche conservatism and ecological filtering as factors triggering the observed changes on individual axis of the trait space (as done in ***Chapter 2***, ***4*** and ***7***); and second on the importance of changes in (or escape from) the factors constraining the trade offs between correlated traits (as assessed in ***Chapter 7*** and ***5***).

Perhaps, the most likely mechanisms causing the observed patterns of trait adaptation in aliens is a combination of niche conservatism (as evaluated in ***Chapter 2*** and ***7***) and phenotypic plasticity (Ackerly 2003). For non–natives, trait variation by phenotypic plasticity, would allow adjustments in their expressed traits, so that there is a better match between performance and environment (hence a conservation of their fundamental niche). This process could be favoured by the escape (or strength reduction) from a

series of constraining costs known to limit the levels of trait variation (e.g. herbivory–parasitism, close competition with co–evolved plants, or investment in defence mechanisms). This can potentially reduce the strength of selection (Donohue 2003), or/and alter the strength of ecological interactions (mainly predation and intense competition) within their new community.

Studies assessing the role of phenotypic plasticity on invasion success have indicated a higher plasticity of alien species when compared to natives (as reviewed by Daehler 2003). From them it could be concluded that aliens often have a wider physiological responses (Pattison, Goldstein & Ares 1998, Williams & Black 1994), bigger changes in biomass allocation patterns in response to different environmental conditions (Baruch & Bilbao 1999, Simoes & Baruch 1991, Yamashita, Ishida, Kushima & Tanaka 2000) and/or larger variation in patters of germination (Hierro et al. 2009). Probably this mechanism is what allows non–natives to establish and prevail, while conserving their niche and possibly their mean trait value. Nonetheless, it is important to point that this does not imply an *a priori* performance advantage of aliens over natives, just a change in certain attributes related to plant performance. Furthermore, it is clear the necessity to couple this phenotypic variation with the level of genetic variation in order to assess the possible responses of an alien species to environmental changes over time or space.

In addition to phenotypic plasticity, anthropogenic selection resulting from intentional or unintentional introductions is also a key factor determining the level of aliens trait variation, selection and change (Alpert 2006, Thuiller, Richardson, Rouget, Proches & Wilson 2006). In the case of intentionally introduced species, most of them have been selected for their usefulness to humans with a special interest in species with horticultural and/or agronomic uses. This screening process has also aimed to select certain traits within these species. Specifically species or genotypes with fast growth, high resource efficiency, faster generation times, high reproductive output, or high resistance to pathogens have been usually selected for human use (Alpert 2006, Thuiller et al. 2006). Unintentional introductions also impose a set of filters to the introduced community. These filters select a non–randomly set of traits which increase the probability that an alien can be transported along with commercial goods, human belongings, or transport vessels. Most of these characteristics (e.g. high propagule number, dispersal by animals, parasitism on intentionally introduced organisms, tolerance of extreme conditions) are highly correlated to human activity or human modified habitats (Alpert 2006, Leishman & Thomson 2005, Leishman et al. 2010) enhancing their probability of establishment success in human intervened areas. For either of these cases (i.e. intentional or unintentional introductions) successful aliens would most likely express the same attributes in both its native and introduced region, or just vary within its' natural range of phenotypic plasticity.

These factors (i.e. phenotypic plasticity, niche conservatism and human selection of attributes) could potentially drive alien species attributes to represent states at the edges of previously described global domains of trait distribution (Falster & Westoby 2003, Moles et al. 2006, Moles & Westoby 2006, Wright et al. 2004). This use of areas at the extremes of the trait domain was observed in our results (***Chapter 3***, ***4*** and ***5***)

as indicated by the location and skewness of the observed alien mean trait values and distribution, which significantly differed when compared to the native community. This links to the mechanism discussed next, the escape of biophysical costs.

Phenotypic plasticity and anthropogenic selection might enhance or direct the patterns of trait variation. The effects of "biophysical costs" (or in the case of aliens escape from them) would then constrain trait variability by establishing a space of viable traits–combinations (or "trait envelope). As discussed in the introduction, a multidimensional trait spectrum is limited by a set of biophysical costs (e.g. physical properties of the tissue, biotic milieu, environmental factors, disturbance regimes, etc.) and evolutionary processes (e.g. trait co-evolution) that creates what could be considered a community "trait envelope" (***Fig. 8.2***). This represents (as presented in ***Fig. 8.2***) the balance between the possible advantages and disadvantages of being in one end or the other of an ecological strategy. All else being equal, the trait space from alien colonisers should be restricted by the same factors (trade–offs, evolutionary and physiological constrains) that limit natives (as shown in ***Chapter 5*** and by Leishman et al. 2007, Leishman et al. 2010). But as predation pressures are reduced, due to aliens escape from predators–parasites, non–natives can then occupy spaces far from the native species' physiological–cost effective optima. As a result, the new alien population would experience strong selection for shifts on more than one trait axis, due to the coordination specifying an ecological strategy (that is a movement along the strategy axis; as shown in ***Chapter 5*** and schematised in ***Fig. 8.2***).

Some of the major hypothesis explaining the advantage of aliens over native species, such as the enemy release hypothesis (Colautti et al. 2004, Torchin & Mitchell 2004), novel weapons (Callaway & Aschehoug 2000, Callaway & Ridenour 2004), invasion meltdown (Richardson, Allsopp, D'Antonio, Milton & Rejmanek 2000, Sax, Stachowicz & Gaines 2005, Simberloff & Von Holle 1999) or the empty niche (Elton 2000, Hierro et al. 2005), etc. are related to the escape from one or more "biophysical costs". Therefore, understanding the consequences of these factors on the trait variation of aliens would be useful for determining both the causes and consequences of escaping the limitations imposed to traits variation.

Is clear that large mixture of mechanisms may underlie invasion success (Levine, Vila, D'Antonio, Dukes, Grigulis & Lavorel 2003), and the ones proposed here are only based on theoretical backgrounds or indirect evidence from studies in the field of trait evolution/differentiation. But as suggested by the evidence summarised in this dissertation and other similar studies (e.g. Crawley et al. 1996, Gonzalez et al. 2010, Lake & Leishman 2004, Leishman & Thomson 2005, Ricciardi & Atkinson 2004, Scharfy, Funk, Venterink & Gusewell 2011, Strauss et al. 2006, Thompson et al. 1995, van Kleunen et al. 2010, Williamson & Fitter 1996), a key element to understand the success of non–natives in their introduced range is considering the functional or phylogenetic relatedness between the alien and native community, and its relation to differences in plant performance.

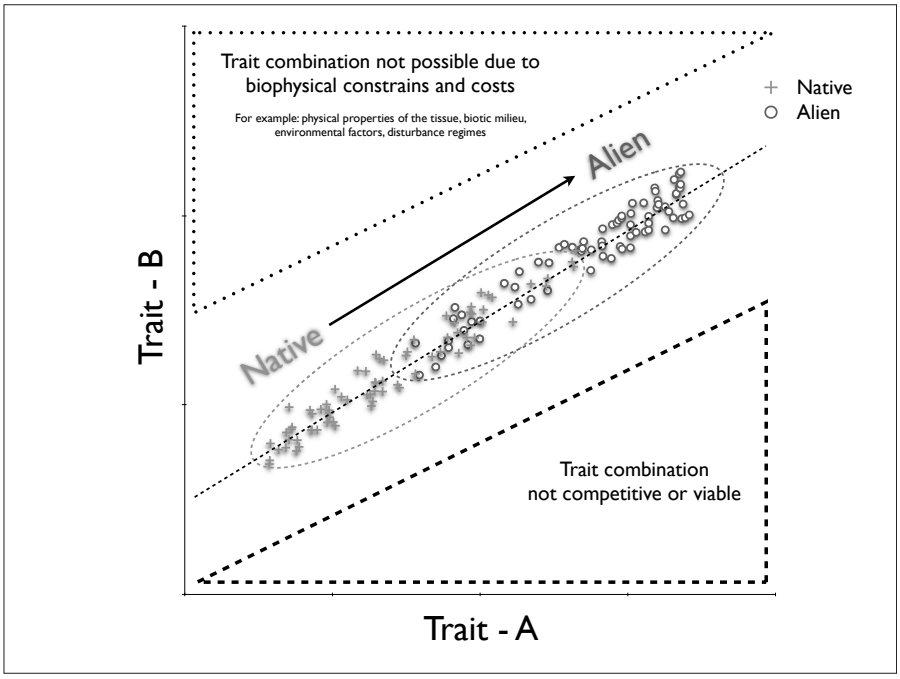

Figure 8.2 Shift between alien and native plants along an ecological strategy. Due to the evolutionary and physiological constrains imposed to both individual traits and its trade-offs with related attributes (which define the ecological spectrum of interests), alien and native species are expected to fall within the same ecological strategy (no changes in the relations between related traits). We show how aliens have trait combinations shifted towards the extreme of the native trait envelope define by the ecological strategy.

8.4 From patterns to mechanisms: Linking trait convergence–divergence to hypothesis explaining alien success

Various hypotheses have been proposed to explain which species would be successful once introduced. These are based on how differences or similarities in life history attributes determine both the demographic success (e.g. long–term and large–scale positive or stable population growth) and the ecological impact of an introduced species. Methodological approaches used to determine both of these aspects could be grouped as either focusing on either the characteristics of invaders (e.g. Kolar & Lodge 2001, Pyšek & Richardson 2007, van Kleunen et al. 2010); properties of the invaded community (e.g. Blumenthal 2005, Davis et al. 2000, Hufbauer & Torchin 2007, Keane & Crawley 2002, Shea & Chesson 2002); or evolutionary processes (e.g. Diez et al. 2008, Duncan & Williams 2002, Ellstrand & Schierenbeck 2000, Maron, Vila & Arnason 2004, Rejmanek 1996, Strauss et al. 2006, Thuiller et al. 2010). The goal of this section is to establish a link between the patterns of traits (dis)similarity reported in this dissertation,

and some of the most accepted species, community and evolutionary based hypotheses used to explaining alien species success.

8.4.1 Species based hypothesis

As discussed previously, efforts to determine the attributes of successful aliens has yield numerous generalisations on the question *"what makes an alien successful?"*; and multiple hypotheses aiming to explain these patterns (reviewed by Sax & Brown (2000), Hierro et al. (2005), Mitchell et al. (2006) and Hufbauer & Torchin (2007), and summarised as species hypotheses in ***Table 8.1***). Species based hypotheses suggest that aliens are either inherently superior than natives (e.g. inherent superiority and novel weapons hypotheses); or that aliens are only successful in areas where they are sufficiently different to the native community, so that they avoid competition (e.g. empty niche and enemy release hypotheses). In the first case, this means a generalised differentiation between plant groups, especially in axes of ecological variation related to competition, reproduction and/or growth (as shown in ***Chapter 2*** for multivariate trait composition and in ***Chapter 5*** for individual leaf traits). Other works have also addressed this conception of generalised superiority of aliens, based on measures of competition (Callaway & Aschehoug 2000, Sax & Brown 2000) or defense mechanisms (Callaway & Ridenour 2004, Vivanco et al. 2004). Nevertheless, is clear that this is only a first order approach to understand the success of aliens, given that a particular differentiation in attributes is not advantageous under all situations (having a 10% larger leaf, does not have the same implication in a desert than in a tropical rain forest).

The results presented in ***Chapter 3*** and ***5***, support the idea of inherently superior of an alien when compared to co–occurring natives. Of particular interest are those finds relating to traits associated with carbon capture strategies (i.e. traits of the "leaf economics spectrum" compared in ***Chapter 5***). These indicate how alien species are successful not because they have different resource acquisition strategies or lower nutrient requirements than natives. Rather, it seams that the suite of traits expressed by these species provides them with a competitive advantage from co–occurring natives (e.g. higher specific leaf areas, shorter life cycles, devote more resources to reproduction and produce more seeds that are better dispersed and germinate faster). Nonetheless, the large variability of alien–native differences across sampled locations suggests how site conditions are what ultimately determine the level of differentiation between these groups (as shown ***Chapter 3***, ***4*** and ***5*** by a significant effect of sites in trait comparisons). As a result any performance advantage of an alien with respect of co–occurring natives is site specific.

The idea of site–specific advantageous trait combinations was supported by both the significant, and positive relation, of leaf traits and resource availability gradients (***Chapter 5***) and the scale dependence of the differentiation between natives an alien species (***Chapter 4***). Although it was not possible to address the effect of changes in the biotic–milieu (composition of direct competitors, herbivores and parasites) due to lack of adequate information; it was hypothesised that the escape from enemies by aliens, once introduce to a new area, enhances and possibly causes the differences

between alien–native species. This will be especially the case for areas with high resource/disturbance rates, as suggested by Blumenthal (2005), due to possible higher performance gains (moving to the fast end of the resource acquisition spectrum) from enemy release in high resource/disturbance areas. It is clear that there is a need for large scale field based conspecific comparisons, aiming to evaluate how alien species in high resource/disturbance situations are more strongly released from enemies than those under lower resource/disturbance conditions.

8.4.2 Community based hypotheses

The species assembly in a given plant community can be perceived as the result of the interaction between the conditions of the area in which a species arrive (such as resources, climate and disturbance), when they arrive (time of introduction and subsequent re–introductions), and how these interact with both its' environment and each other (balance between competition–herbivory–parasitism). Species introductions fit in this scheme, as new colonisers face the same constrains as natives do for establishing suitable populations in to particular communities (***Fig. 8.2***). Based on these principles, several hypotheses have been proposed to explain alien species success (e.g. biotic resistance hypothesis, fluctuating resources, and the resource–enemy release hypothesis, as discussed in ***Chapter 1***). These ideas focus on the attributes of the community where a given alien species is introduced, aiming to determine how these factors relate to the likelihood of that location being invaded. In this dissertation two alternative hypotheses linking community properties to aliens success were considered: the biotic resistance and the resource–enemy release hypothesis.

The biotic resistance hypothesis, is one of the oldest principles in invasion ecology (Elton 2000). It's based on the idea that communities' with high species diversity are less likely to be invaded. Most studies testing this hypothesis have focus on how aliens will interact with resident species (mainly competition) and the level of saturation of the recipient community (availability of niches). However, the results from these comparisons have been inconclusive, showing both positive and negative relations between diversity and probability of alien success (as reviewed in Levine et al. 2004, Sax & Gaines 2003, Shea & Chesson 2002). This discrepancy has been usually attributed to the scale dependence of diversity patterns (Sax & Gaines 2003, Sax et al. 2005).

Alongside the scale dependence of this relation, an alternative explanation of this discrepancy is the effect of diversity on the balance between resource supply and availability in a site. As experimental studies have shown (Fukami 2001, Levin 2000), the number of species using the available resources determine the resource availability (i.e. density of unused resources as nutrients and water) of a location, and it in turn would determine the possibility of successful introductions (resource opportunities as described in Shea & Chesson 2002). For example, diverse communities will contain species with a grater range of traits, thus making the use of resources more efficiently (proposed by the resource use complementarity hypothesis Loreau & Hector (2001) and discussed in ***Chapter 3***). As a result of this, a limited supply of resources would be available for aliens to tap in (i.e. a reduced resource availability). The same effect could also be

caused if these diverse communities contain species with traits that allow them to use resources either more efficiently or at a faster rate, as proposed by the sampling effect hypothesis (Tilman 1999), so that the reduction in the resource supply poll is reduced to suboptimal levels for aliens.

An alternative view on the effect of available resources and alien success is the resource–enemy release hypothesis. This idea, originally proposed by Davis et al. (2000) and adapted by Blumenthal (2005), builds from the association between alien species success and environmental conditions, resource availability , disturbance, and release of enemies. The principle of this hypothesis is that a plant community with unused resources (such as water, nutrients, space or light) will be more susceptible to introductions (as tested in ***Chapter 5***). The pool of unused resources will be then determined by the balance between the supply and uptake of these by the resident native community. As conditions (climatic and nutrient availability) are not fixed over time, fluctuation in the resource availability will create windows of opportunity for invasions (as reviewed by Davis et al. 2000). Additionally, the scape from predators and/or parasites could affect the benefits of higher available resources synergistically. This synergy between biotic and abiotic factors is centred on how changes in predation–parasite pleasures or *'escape opportunities"* (that is low level or low efficiency of natural enemies to which aliens might be susceptible) might provide a greater benefit for species adapted to high–resource conditions (Blumenthal 2005). This is typically the case of plants growing in resource rich areas, where they are typically fast growing, and not well defended against enemies.

Test of these ideas in ***Chapter 5*** showed how performance of native and alien plants is associated to resource availability gradients. Evidence for this was the significant relation between alien and native traits (and position along the carbon–strategy spectrum) and gradients of soil fertility and disturbance (***Chapter 5***). This, in combination with the consistent carbon strategy of aliens and natives along the same global resource and disturbance gradients (Leishman et al. 2007, Leishman et al. 2010), indicate how given the adequate conditions, any given species could and would be successful when introduced. As a result, the success of a given introduced species is then not dependent of area of origin; but rather, it is determined by it having a suite of traits enabling to exploit the new habitat and the biotic–abiotic–disturbance setup it's confronted with (Thompson & Davis 2011).

8.4.3 Evolutionary based hypotheses

Several works have recently addressed the link between evolutionary patterns and alien success (e.g. Agrawal & Kotanen 2003, Cadotte et al. 2009, Jiang et al. 2010, Mack 2003, Proches et al. 2008, Thuiller et al. 2010). These pick up on Baker et al. (1965) work addressing the potentially critical role of evolution in the success of colonising species, although important progress has been made, understanding of the evolutionary dimension of this problem remains rudimentary. This is perhaps due to the challenges of both in understanding when and how evolution plays a role in the success of alien species. Additionally, determining a way to measure and interpret patterns emerging

from these evolutionary processes has also proven to be challenging. Irrespective of these problems, the known impact of evolutionary processes on the fitness of introduced individuals makes the evaluation of this dimension necessary for predicting successful introductions.

The influence of evolutionary process on aliens' success might be in from of competitive advantages when compared to co–occurring natives (addressed in ***Chapter 4*** and ***6***), or performance differences between the introduced and native range (addressed in ***Chapter 2***). In this dissertation, two of the most important theories linking the level of similarity in attributes and the success of aliens (e.g. evolution of increased competitive ability and Darwin's naturalisation hypothesis) were examined.

The evolution of increased competitive ability proposes that in the new area, changes in the selection pressures (due to founder effects, genetic bottle necks, hybridisation, genotypic plasticity, etc.) will drive changes in performance attributes. A particular case of this is the investment in costly defences against enemies, which would no longer enhance fitness if aliens escape from natural enemies in the new area. Results from meta–analyses in this dissertation (***Chapter 2*** and ***Chapter 7***) consistently supported the trait conservation hypothesis and not the evolution of increased competitive ability hypothesis. It's shown in ***Chapter 2***, how traits of con–specifics, closely linked to key ecological strategies of plant performance, are consistently similar between the native and introduced range. This pattern was also observed for other studies (as summarised in ***Chapter 7***). Together this would suggest that traits are conserved along the trait spectrum, as no differences in evaluated attributes of non–natives was detected between their native and alien, naturalised and invasive ranges.

Although the analysed attributes in this dissertation show a consistent conservation across space, it is not implied that aliens do not have the potential to phenotypically or genetically adapt to the new conditions they might encounter in their new habitat (as we explain in ***Chapter 2***). It's considered that traits on a site are the result of the balance between long–term evolutionary inertia pushing towards the conservation of traits (Rejmanek 1996), and short–term adaptation to biotic interactions, environmental stochasticity and phenotypic plasticity that favours trait variation [such as core physiological and genetic constrains which shape the fundamental niche, as presented in Grime (2006) and Webb et al. (2002)]. In other words, those traits that have been shown to be highly conserved over evolutionary time (e.g. wood density, seed mass, SLA, leaf life span) will be more conserved across ranges than those that are highly influenced by biotic, ecological or environmental gradients (e.g. canopy transpiration, rhizome re–sprouting, height, relative growth rate).

Darwin's naturalisation hypothesis on the other hand, links evolutionary dynamics to the level of similarity between aliens and co–occurring natives. It states that closely related species will overlap more in their niches (and therefore in their traits) than less related species (Rejmanek 1996, Thuiller et al. 2010). As a result novel genera would be more successful in colonising new ranges than genera with native representatives. An alternative formulation of the role of phylogenetic relatedness and niche overlap is termed the phylogenetic attraction hypothesis (Webb et al. 2002). It argues that intro-

duced aliens that are closely related to native residents might have improved chances of naturalising as they share similar pre–adaptations to the local environmental conditions.

Analyses presented in ***Chapter 2*** and ***7*** indicate that alien species showed, when compared to co–occurring natives, a tendency to phylogenetic clustering (i.e. closely related species co–occurring on a site), therefore supporting the predictions of the phylogenetic attraction hypothesis. This similarity was consistent also for comparisons controlling for spatial scale (***Chapter 4***). The evidence presented in this dissertation provides strong support for the importance of evolutionary patterns and the need to account for phylogenetic relationships when examining alien invasions, especially when the goal of the study is to predict which alien species might be successful.

By examining global distribution patterns of native and alien species traits, this work has shown how the observed distribution of alien plant communities is the likely results from two mechanisms. First, alien species showing an evolutionary conservation of traits, restricting them to areas that match the environmental conditions of their native habitat (for reviews and meta-analysis of this topic see Cahill Jr, Kembel, Lamb & Keddy 2008, Pyšek & Richardson 2007). Second, the environmental conditions of the new habitat would filter out unsuitable aliens, therefore allowing only those species with traits similar to native species to colonise (Wiens et al. 2010, Wiens & Graham 2005).

8.5 Final conclusions: where do we stand and where does the road ahead lead to?

Invasion biology research agenda has reached an exciting point. The combined effort of large numbers of individual case and community studies has allowed the production of several testable hypothesis while setting the ground for theoretical advancement. Additionally, the study of introductions has provided a unique, but unfortunate, opportunity to address the possible ecological and evolutionary mechanisms behind both species distribution and community assembly patterns (Callaway & Maron 2006, Shea & Chesson 2002). The scientific importance of this reaches far beyond the field on invasion biology.

In this work it has been shown, in a fairly robust way, that alien species have a combination of traits that significantly differs from those of the native community where they are introduced, hence supporting the classic empty niches' idea to explain invasions. Meanwhile, the attributes of these successful aliens show no significant change between ranges, indicating that the observed pattern of trait conservatism between ranges originates from core ecological, physiological and genetic constrains. These trends were consistent when the dissimilarities between plant types were evaluated in a community context (comparison of co–occurring aliens and natives) and when the spatial scale of this community context (i.e. how a community is defined) was taken in to consideration. Together, the evidence presented here very clearly indicates how the role of plant traits in the colonisation process of aliens is to a very large extent context specific (biogeographical–environmental–evolutionary). As a result, traits that might confer an

advantage in a given community might be neutral or even detrimental in different conditions.

The road ahead for invasion biology should be paved on all the available biogeographical, environmental and evolutionary information, and should aim to link life history, community characteristics and evolutionary processes. For this some key factors must be carefully considered:

Appropriate spatial scale: Ecological and evolutionary mechanisms act at particular scales. This makes the use of multi–scale contrast the best approach to evaluate the influence of all possible mechanisms driving introduction success.

Appropriate phylogenetic scale: Framing the comparison between aliens and natives in an adequate context is relevant. To which species or group of these are aliens contrasted; also the phylogenetic background of the community they are embedded is important to determine the possible mechanism driving the observed patterns.

Appropriate measure of (dis)similarity: Both functional and phylogenetic information should be considered in the quantification of the dissimilarity between aliens and natives.

The work presented here is a contribution to the long lasting quest for understanding the causes and mechanisms behind the species invasiveness–community invasibility continuum. This dissertation aimed to link three separate lines of evidence that have received considerable attention independently (species invasiveness, community invasibility and evolutionary patterns). It is clear that if the ultimate goal is to predict invasion risks (by a species or of an area) these three dimensions must be accounted simultaneously